

VISUAL BRIGHTNESS DISCRIMINATION OF THE JUMPING SPIDER *MENEMERUS BIVITTATUS* (ARANEAE, SALTICIDAE)

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ABSTRACT. It was observed that the jumping spider *Menemerus bivittatus* lives on light surfaces as well as on dark surfaces, hunting prey which is lighter or darker than the surface the spider is on. From these observations arises the question about the brightness or contrast discrimination abilities of this spider. The orientation response was recorded for 14 spiders to a moving circular prey-stimulus varying from white, through grey, to black, against a white, grey or black background. When the stimulus was darker than the background, there was a rapid increase in response as the stimulus gets darker. This rapid change in response with stimulus brightness did not occur when the stimulus was lighter than the background. These results reveal a high contrast discrimination ability and also a dependence of the response on the overall stimulation conditions.

The visual system of jumping spiders (Salticidae) is highly developed when compared to other families of spiders. Like most spiders, jumping spiders have four pairs of eyes. The most specialized are the anterior median eyes (AM), that are used in prey pursuit (Land 1971). It has been suggested by Land that the AM are capable of color vision. The other eyes function primarily to detect prey movement and to elicit orientation toward prey (bringing the prey into the visual field of the AM eyes).

The jumping spider *Menemerus bivittatus* (Dufour) is common in Southern Brazil and can be found throughout the year in almost all homes of São Paulo. Retreats are generally located in the highest part of doors or window frames or under an outside overhang.

Preliminary observations of the habitat preferences of *M. bivittatus* revealed that (1) spiders hunted on either a dark surface (e.g., black painted poles) or a light surface (e.g., wall of buildings) and (2) on both of these surfaces both light colored prey (e.g., small Diptera) and darkly colored prey (e.g., *Musca*) were taken. There appeared to be no difference in prey catching efficiency between the different backgrounds. Since *M. bivittatus* has a light appearance (greyish brown with black stripes) the spider is very conspicuous on a black ground and almost invisible on light colored walls.

These observations raised the question of whether jumping spiders are capable of discriminating differences in contrast between stimulus and background. Since single visual receptor cells are known to react with graded potentials to light

intensity, the physiological capability for contrast discrimination appears available. The most likely mechanism is a neural circuit that enhances brightness differences and contrast in the same way as is known for many vertebrates and invertebrates. However, the question remains on how contrast discrimination is integrated into specific behaviors, such as prey catching and mate recognition. The reflexive behavior of jumping spiders to orient themselves and the AM eyes toward the prey after its detection by the secondary eyes (Land 1972) is a very simple behavioral response that can be easily observed and recorded in the laboratory.

The purpose of this experiment was to establish the psychophysical brightness discrimination function measured by this orientation response for different levels of ground brightness. Another question was to find if the function for the discrimination of a light stimulus against a dark background is symmetrical to a dark stimulus against a light background. Lack of symmetry between the functions would indicate an increased ability at prey detection in one of the situations and might suggest that the spider would have a preference for one of the hunting conditions.

METHODS

Subjects.—Ten adult female and four adult male jumping spiders, *Menemerus bivittatus*, were collected on the campus of São Paulo University and taken to the laboratory where they were held individually in petri dishes in 12/12 h light/dark illumination. Individuals ranged from 6–12 mm

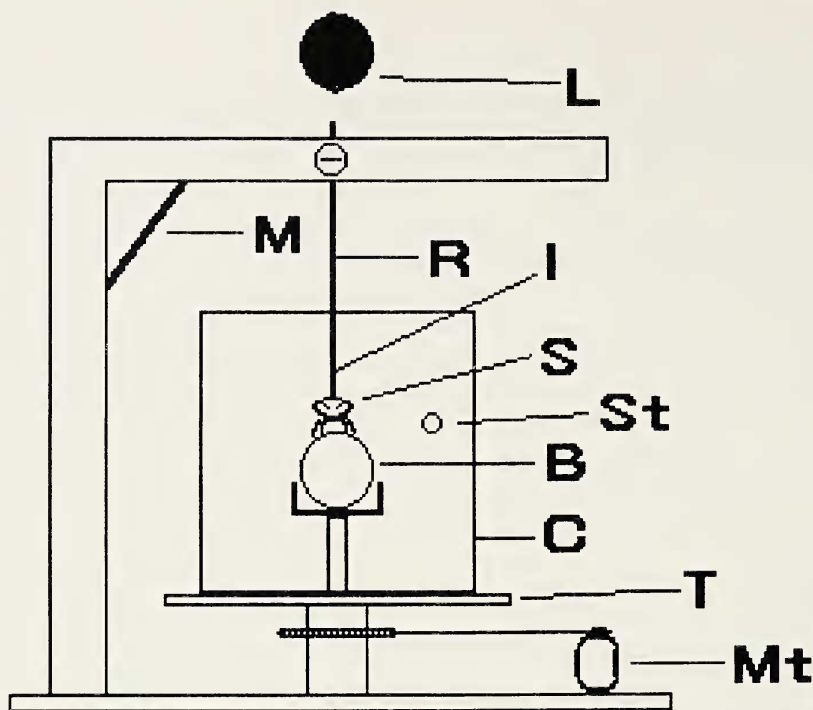


Figure 1.—Apparatus used in the experiment. The spider (S) after being anesthetized was glued to the head of the insect needle (I) that was inserted into the rod (R) that was adjusted so that the spider touched lightly the styrofoam ball (B). Around the spider the painted cylinder (C) with the stimulus (St) that could be easily interchanged, was positioned on the revolving turntable (T) driven by the motor (Mt). Observation was made through the mirror (M). The lamp (L) provided constant and uniform light of 155 lux measured at 90° on the surface of the styrofoam ball.

in total length. Live *Musca* were offered to each spider once a week. The spiders survived for several months under these conditions making it possible, if necessary, to divide the whole experimental procedure into several experimental sessions on different days.

Experimental procedure.—Prior to an experimental session the spider was lightly anesthetized with carbon dioxide so that the head of an insect needle could be glued with wax to the rear part of the prosoma. Care was taken to avoid covering the eyes with wax. After the spider completely recovered from anesthesia, the animal was placed into the experimental apparatus (Fig. 1). The experimental apparatus was basically a motor driven turntable on which three different cylinders, constituting the background for the visual stimuli presented to the spider, could be made to turn in either direction. On the axis of the cylinder a styrofoam ball (25 mm in diameter) lay loosely in a Teflon cup. The spider, held by the needle glued to its prosoma and an adjustable rod, could walk on the styrofoam ball in any

direction, turning or rolling the styrofoam ball. The slightest turning or walking movement of the spider (and consequently of the styrofoam ball) could be observed through a mirror attached over the apparatus. Observation through a mirror was preferred to direct observation in order to reduce disturbances of the spider. Overall illumination was provided by a daylight ring light (Toshiba, Japan) producing an illumination of 155 lux at the top of the styrofoam ball at 90°.

White, grey and black glass cylinders (250 mm diameter, 300 mm height) were used for the background against which the spider could see the stimulus. The white cylinder had a reflection density of $d = 0.11$, the grey 0.56, and the black of 2.08. Density was measured with a reflection densitometer (X-Rite Inc., Grandville, Michigan, USA, Model B318) calibrated for $d = 0.00$ with a standard calibration card (TiO₂ coated). The glass cylinders were painted from outside (so that the inner glare was the same) except for an 8 mm diameter "hole" left transparent, coplanar to the spider, where the stimuli could be

Table 1.—Mean and SD of the response probability for the white, grey and black backgrounds for each presented stimulus. $n = 14$ for all cases.

Stimulus density	Background					
	White		Grey		Black	
	mean	SD	mean	SD	mean	SD
0.11	0.01	0.00	0.09	0.06	0.52	0.09
0.27	0.13	0.05	0.15	0.12		
0.31	0.29	0.09	0.15	0.12	0.59	0.08
0.36	0.39	0.15	0.14	0.09		
0.50	0.78	0.09	0.00	0.00	0.53	0.10
0.56	0.80	0.14	0.00	0.00		
0.58	0.86	0.12	0.00	0.00	0.46	0.11
0.76	0.90	0.09	0.85	0.05		
0.86	0.94	0.06	0.93	0.03	0.38	0.07
0.91	0.98	0.02	0.96	0.02		
1.01			0.99	0.01	0.33	0.08
1.15					0.25	0.07
1.52					0.18	0.07
2.08					0.08	0.03

applied from outside without producing any shadow or border. The stimulus thus subtended an angle of about 4° at the spider's eyes. With the white background, stimuli of the following reflection densities were used: 0.11, 0.27, 0.31, 0.36, 0.50, 0.56, 0.58, 0.76, 0.86 and 0.91. With the grey background the same stimuli were used, and also a darker one of 1.01 reflection density. For the black background, stimuli of the following reflection densities were used: 0.11, 0.31, 0.50, 0.58, 0.86, 1.01, 1.15, 1.52 and 2.08. The stimuli were produced by painting white paper with the same paint used for the glass cylinders, mixing from the white and black paint in different quantities.

Each animal was tested for the white, grey and black backgrounds but in different orders. For each background the stimuli were presented in random order. Five trials were run on each stimulus/background combination. Each trial consisted of five complete turns of the cylinder (alternating left and right turns). Each turn was started with the stimulus exactly behind the spider's back, out of its visual field (this could be verified by the fact that the spider never responded to a moving stimulus at that position) and took around 20 seconds to be completed, resulting in a mean angular velocity of the stimulus of 18 deg/s. For every turn of the cylinder it was manually recorded if the spider made a response toward the stimulus or not. For each density val-

ue of the stimulus the overall response probability was calculated by dividing the number of cylinder turns that elicited a response by the total cylinder turns. With few exceptions, there was no doubt that a movement of the spider was directed to the moving dark or light spot. When, for some reason the spider entered spontaneous walking activity, the experiment was interrupted until the spider assumed its typical alert posture.

After finishing the stimuli presentations for one background density, the same procedure was repeated for a different cylinder. The spiders stayed responsive for up to 3 or 4 hours.

RESULTS AND DISCUSSION

The mean and the standard deviation (SD) for the response probabilities for each background and stimulus are given in Table 1. The SDs calculated among animals are fairly small, suggesting that the recorded orientation response is rather reflexive. The response probability curves for the white, grey and black backgrounds are given in Fig. 2.

The response curve for the white background varies from almost zero for a white stimulus (zero contrast with the background) to almost 100% for a 0.91 stimulus density (maximum contrast). This experimental condition would conform to a situation where the spider hunts for dark prey on a light background, which seems to be the situation to which the spider is best adapted, since the spider itself has a light color and most of the prey like *Musca* are dark in color.

The response curve for the black background has a quite different shape, not being just the mirror image of the first curve as might have been expected. Response probability declines very slowly with increasing stimulus darkness. The highest response probability is somewhat lower than 60% for a light grey stimulus (reflection density of 0.27). For a lighter stimulus (0.11) that produces a higher contrast with the black background, the response rate is even lower. The difference is statistically significant (Student, $df = 13$, $t = 2.57$, $P < 0.05$). Of the 14 spiders tested, 12 presented a lower response rate for the brighter stimulus. This suggests that the spider is not responding just to the contrast value between stimulus and background. The spider might be responding in part to the appearance of the stimulus disregarding the background, or some other unknown factors are influencing its behavior.

The response curve for the grey background shows, as expected, the lowest response proba-

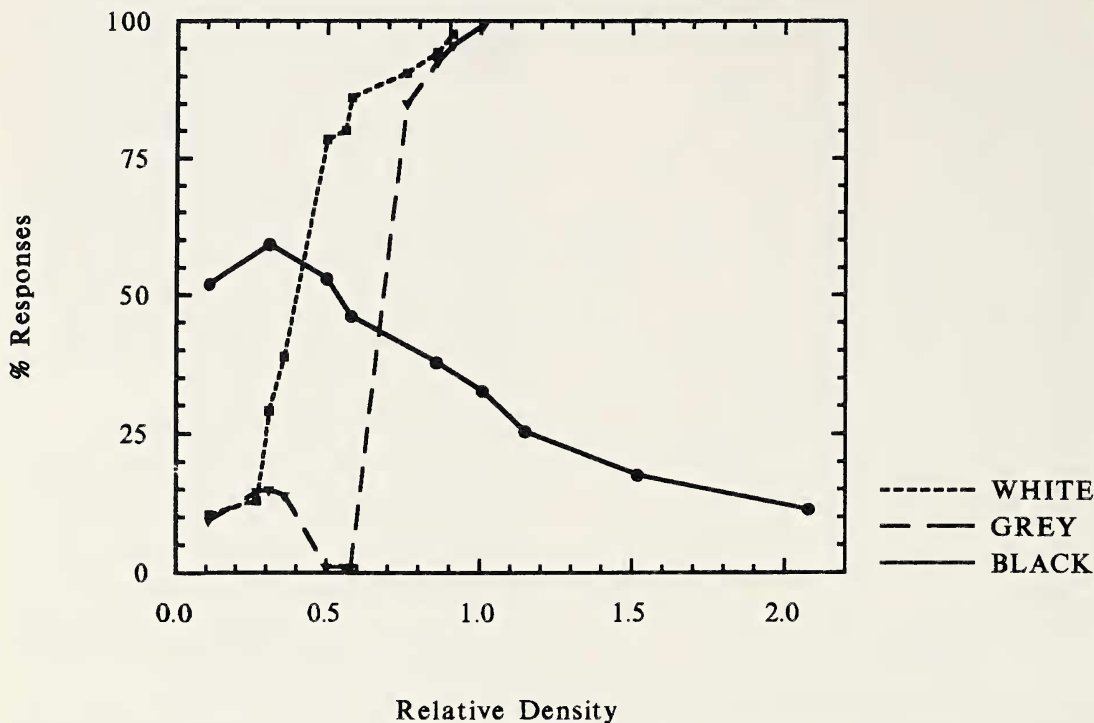


Figure 2.—Response probability curves for the white, grey and black backgrounds (cylinders) to stimuli of different greyness, from white to black.

bility for the stimulus density that equals the background density (relative density of 0.50, 0.56 and 0.58) where the contrast is close to zero. The part of the curve where the stimuli are darker than the background has more or less the same shape and steepness as the curve for the white background. With reversed contrast, the highest response probability is again not for the highest contrast condition, but for stimuli in the relative density range of 0.27–0.36. Out of the 14 records, for nine the response rate for the lightest stimulus (0.11) was lower than for the next darker one, two were equal and three reversed. The Student test for the difference of the means for both stimuli revealed a near to significant probability ($df = 13$, $t = 1.98$, $P > 0.05$). These results favor the idea that the response is not only guided by the contrast between prey and background, but also by the absolute lightness of the prey.

The lower response maximum of 60% for the stimuli against the black background could suggest that the spiders are visually less alert or aroused in this situation since the overall light level within the black cylinder must be lower, due to less reflection of the constant illumination provided by the lamp on the top of the cylinder.

If this were the case, visual alertness would also be lowered with the grey cylinder. Since in the grey cylinder a response rate of 100% was achieved for darker stimuli, visual alertness differences, if any, caused by different illumination levels, do not explain the results.

These overall results could be compared to the description of Land (1972) who, in an experiment where jumping spiders responded to black or white stripes, found that the pursuit response to black stripes was given to the leading edge, while the response to white stripes to the trailing edge. Land concluded that the stimulus must always move in such a way as to cause sequential darkening of adjacent photoreceptors. The results of the present experiment could be explained in the same way, since the spider could be responding to an edge of the stimulus, although the stimulus was small. For the light stimulus on the dark background, the spider would be responding to the trailing edge of the stimulus or, what would be exactly the same, to the leading edge of the dark background. This would mean, that the stimulus is now the “huge” background which of course had lost its “prey characteristics” to the spider, explaining the lower response rate

for this condition. An alternative interpretation would be that the spider in this experiment is reacting to the small stimulus as a whole, as long as it has enough contrast with the background, but with a clear preference for dark stimuli on lighter backgrounds. Drees (1952) showed that the courtship behavior of *Epiblemum scenicum* (Salticidae) reveals well-developed visual acuity. Such acuity might also be important in prey capture. However, Blest (1985) found that the prey capture sequence could be elicited by stimulus shapes quite different from normal prey, as in the study reported here. Therefore, it seems that the orientation response which initiates both prey capture and courtship is mainly guided by the contrast of the stimulus against the background.

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